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GROWTH AND LONGEVITY OF THE „LIVING FOSSIL“
CONGERIA KUSCERI (BIVALVIA: DREISSENIDAE)
FROM THE SUBTERRANEAN DINARIC KARST OF CROATIA

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ABSTRACT

The present study analyzed growth and longevity of the endemic cave dwelling bivalve Congeria kusceri obtained from the pit Jama u Predolcu, Croatia. A water temperature of 13-14°C constituted the lower limit for shell growth of C. kusceri. Obtained data also indi-cated that enhanced calcium uptake by C. kusceri during its summer growth and reproductive phases coincided with a decrease in alkalinity of the pit water. An analysis of shell growth rings in C. kusceri has identified an impressive longevity of 53 years. Calculations of growth rate suggested maximum theoretical shell lengths (L.) of 16.7 mm for males and 18.7 mm for females and a growth constant of 0.04 year-1 for both sexes. Congeria kusceri can, however, grow to a shell length of > 24 mm, suggesting that longevity of this species could be greater than that identified in this study. The obtained results add to our understanding
of how colonisation and continued and successful occupation of a subterranean freshwater habitat has been achieved.
Key words: Cave-dwelling bivalve, age, longevity, life-history trait.

INTRODUCTION

The amount of energy allocated to growth
is a fundamental feature of an organism’s life
history evolution and diversification (Haag &
Rypel, 2010). Bivalves are one of the most
diverse group of animals and offer a rich variety of lifestyles, adaptations to specific environ-mental conditions and corresponding aging strategies (Abele et al., 2009). According to Philipp & Abele (2010), bivalves have vastly differing maximum life spans ranging from 1 to hundreds of years. The wide variations in age and growth of bivalves show that they employ a diverse array of life history strategies requir-ing different conservation and management approaches (Haag & Rypel, 2010).
Congeria kusceri Bole, 1962, is of especial conservation importance since it is representa-tive of the only known genus of subterranean, troglobiotc, bivalves and occurs only in the underground lakes, rivers and pits of the Dinaric karst (Morton et al., 1998). Congeria kusceri is an endemic Tertiary relic, with most other

congeners, save for two other newly described species Congeria jalzici. Morton & BilandZija, 2013, and Congeria mulaomerovici Morton & BilandZija, 2013, identified by BilandZija et al. (2013), having become extinct by the end ofthe Miocene (Morton et al., 1998). Accordingly, C. kusceriis regarded as a “living fossil”. Congeria kusceri possesses a unique life history trait including a reproductive strategy characterized by early larval brooding in the ctenidia and secondary juvenile brooding in mantle pouches (Morton & Puljas, 2013). It was suggested by Morton et al. (1998) that such a novel life history trait is related specifically to decadal length lon-gevity. Allthe evidence to date, therefore, points to the possession by C. kusceri of an unique suite of characteristics that not only adapt it to life in the subterranean Dinaric karst, but which are wholly different from the thin-shelled, short lived (< 4 years), opportunistic, non-brooding, planktotrophically dispersed, representatives of related dreissenid genera, that is, Dreissena van Beneden, 1835, and Mytilopsis Conrad, 1857 (Morton, 1969, 1989).

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FIG. 1. Map of Croatia showing the location of the study site.

In contrast to the large volume of literature
engendered as a result of the opportunistic and
invasive characters of Dreissena and Mytilop-
sis, this study identifies all of the significant, but
still meagre, research that has been undertaken
on Congeria. In particular, because of their large population sizes, all four of the above species of Dreissena and Mytilopsis have been studied extensively to reveal growth phases and longevities — indicating opportunistic and short life history traits for them all. Conversely, C. kusceri occurs as scattered individuals and clusters in remote subterranean habitats. As noted above, Morton et al. (1998) undertook a study of shell microstructure and estimated the age attained by С. kusceri. That study was, . however, of necessity, limited by the availability of but a few specimens. In 2009, the Croatian Ministry of Environment and Nature Protection, Zagreb, gave permission for the authors to col-lect, monthly, a larger number of individuals of C. kusceri from a readily accessible pit near

Metkovic, Croatia. One of the aims of that study was to examine the reproductive strategy of C. kusceri (Morton & Puljas, 2013). A second component of the study, which is objective of this research and paper, was to obtain: (i), a better picture ofthe growth phases of C. kusceri in the pit and (ii), obtain an estimate, through etched and acetate peel replicas of sections through the shells, of the longevity of this re-markable species.

METHODS

Samples of the stygobiotic bivalve С. kusceri were collected monthly from the pit Jama u Predolcu (Fig. 1), from January to December 2009, to study the reproductive and life history strategies of this protected species (Puljas, 2012; Morton & Puljas, 2013). In addition, measurements of abiotic parameters includ-ing pH, water temperature, dissolved oxygen,

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FIG. 2. Congeria kusceri. The shell of an individual as seen from (A): Right side showing the directions of the sections made for acetate peel replicas (a-b; c-d) and shell length (SL); (B):
The same individual seen from the anterior aspect showing shell height (SH) and shell width
(SW). (U = umbones; L = ligament).

dissolved carbon dioxide, nitrate, phosphate,
chloride, sulphate, degree of hardness and
alkalinity (all following the procedures identi-
fied in American Public Health Association
[APHA],1995) were made on each sampling occasion. This dataset, described in Puljas (2012: 256, table 2) was subjected to t-tests in order to compare the means of nine hydrologi-cal parameters obtained for two periods: (1), the six non-growing and non-brooding (Novem-ber—April) and (2), six growing and brooding (May—October) phases. pH was not analyzed because it did not vary throughout the year, presumably because of karst buffering. Prior to analysis, the data were tested for homogeneity of variance using Levene's test.
The shells of the collected С. kusceri individu-als, subsequent to the removal of the internal tissues for the above reproductive study, were cleaned of epibionts and left to air dry. Infor-mation on shell morphometrics, including shell length (from the umbones to the posterior shell margin, Fig. 2A: SL and a—b), shell height (dorso-ventral axis, Fig. 2B: SH) and shell width (left to right across the valves, Fig. 2B: SW) were obtained for each individual to the nearest 0.1 mm using Vernier callipers.
The archived left shell valves from 40 smaller individuals (2-4 shells month-1) of С. kusceri, ranging in shell length from 6.0-11.0 mm, were used for marginal growth increment analysis

(MGI). Dried shell valves were embedded in epofix resin (Struers), sectioned from the umbo to the posterior shell margin (Fig. 2A: a—b), ground, polished, washed in detergent, air-dried and etched in 0.01 М HCI for 20 min-utes. After washing in water and air-drying, acetate peel replicas were prepared (Richard-son, 2001). Replicas mounted on glass slides were observed under an Axio Zeiss Imager M1 microscope, and photographed with an Axio-Camera (MRc5). The distance between the last clearly visible growth line (Figs. 3A, 3B, arrow) and the shell margin was measured using the Axio-Vision Rel 4.8 program.
Acetate peel replicas of a further 50 individu-als of C. kusceri collected during 2009, with shell lengths ranging from 7.5-17.0 mm, were prepared following the same procedure. Ana-lyzed individuals were selected on the basis of shell length and sex, obtained in the earlier reproductive studies (Puljas, 2012; Morton & Puljas, 2013), to determine differences in growth rates (if any) with respect to sex. Two experienced readers counted independently the numbers of growth lines in the umbonal region of each peel (Fig. 3C). Prior to this analysis, the ages of ten randomly selected shells were estimated from the growth rings in the umbonal region and those in the prismatic shell layer. The obtained numbers were identical, indicating that age can be estimated from both areas.

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Length-at-age data obtained for the C.
kusceri shells were fitted to the von Bertalanffy
growth function L; = L..(1—e-k (tto)), where L; is
the shell length at time +, L.. is the asymptotic maximum length, k is a growth constant and

FIG. 3. Congeria kusceri. (A-B): Photomicrograp-hs of acetate peel replicas of sections through shell margin used for the study of marginal incre-ment analysis; (C): Photomicrograph of acetate peel replicas of sections through the umbonal region. Positions of growth lines are indicated by arrows. Scale bar = 100 um.

ty is the length at time zero (von Bertalanffy, 1938). The FiSAT Il software package version 1.2.2 was used for data analysis. A growth performance index (@’ = log К + 2log L.) was applied to the obtained dataset for comparison of growth parameters with those obtained in other studies (Sparre & Venema, 1998). ANCOVA was used for testing differences in shell length with respect to sex to ascertain any sexual dimorphism, with shell width as a covariate, and for testing differences in the age structure of individuals with respect to sex and with shell length as a covariate.

RESULTS

Hydrology

Ranges obtained for the nine hydrological parameters were as follows: pH (7.0), water temperature (12.5-17.50°C), dissolved oxygen (DO = 1.30-11.65 mg L-1), dissolved carbon dioxide (DCO, = 0.5-4.2 mg L-1), nitrate (NO; = 0.22-0.65 mg L-1), phosphate (POS, = 0.02-0.10 mg L-1), chloride (CI = 16-110 mg L-1), sulphate (SO, = 10-56 mg L-1), degree of hardness (dH = 11.4—16.2) and alkalinity (156— 267 mg CaCO; L-1). Of the nine hydrological parameters tested, however, only differences in temperature (f= 4.929, р < 0.001) and alkalin-ity (t= 3.702, р = 0.004) of the six non-growth and non-brooding and six growth and brooding months were highly significant.
The analyzed dataset thus suggests: (i), there is a threshold water temperature of -13-14°C, from May to October (in 2009), above which both growth and reproduction by C. kusceri take place, and (ii), during the summer period of growth and reproduction, alkalinity values within the pit water were reduced significantly, from 208-267 mg CaCO; 1-1 in the latter period to 156-176 mg CaCO; L- in the former. Comparison of the growth line formation results with environmental water quality pa-rameters showed that water temperature rose from 13°C to 17.5°C in May and decreased from 17°C to 14°C in October. As described above, the difference in temperature means for these two 6-month periods were statistically significant. The decrease in alkalinity from 219 to 173 mg CaCO; 1-1 in May and increase from 156 to 241 mg CaCO; L-1 in October could also be correlated with the duration of the growth season (Fig. 4) and were again statistically significant.

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FIG. 4. Temperature (closed circles, solid line), and alkalinity (open circles, dashed line) variations in the pit Jama u Predolcu.

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FIG. 5. Congeria kusceri. Seasonal variations in the distance between the last growth line
and the shell margin of individuals collected monthly from the pit Jama u Predolcu. Values
are presented as means, standard errors (box) and standard deviations (WHISKER).

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TABLE 1. Morphometric data obtained for Congeria kusceri from the pit Jama u Predolcu during 2009. Values are presented as means + standard deviations (minimum-maximum).

Shell length Shell height Shell width
n (mm) (mm) (mm)

Males 46 NAO? a 2 6.3 + 1.4 ES
(6.6-15.4) (3.7-8.5) (4.0-9.2)

Females 41 11.6 + 3.4 6:04 1,9 o ES,
(6.0-17.0) (4.0-11.6) (3.7-10.0)

Hermaphrodites 2 10.0 + 1.4 03 + 1.8 5.9 + 1.6
(9.0-11.0) (5.0-7.5) (4.8-7.0)

Undifferentiated 1 1.2 4.2 4.0

Total 90 112730 65 = 1.6 8:8 +10
(6.0-17.0) (3.7-11.6) (3.7—10.0)

Morphometric Analysis

The morphometric data obtained for the three measured shell axes of C. kusceri with respect to sex, are summarized in Table 1. Shell lengths of males (n = 46) ranged from 6.6 mm to 15.4 mm, with a mean (+ SD) of 11.0 + 2.7 mm, whereas females (n = 41) ranged from 6.0 mm to 17.0 mm, with a mean (+ SD) of 11.6 + 3.4 mm. ANCOVA showed that there was no significant difference in shell length of animals with respect to sex (ЕЁвв. = 1.52, p = 0.216), that is, C. kusceri is not sexually dimorphic.

Growth Increments

Results of the marginal increment analysis suggested that C. kusceri deposits one growth line annually. Growth lines were present either at the shell margin or close to it for individuals collected in May and June 2009, whereas for a period of five months after June, the distance between the last growth line and the shell mar-
gin generally increased (Fig. 5).
Of the 90 individuals of С. kusceri examined
in this study, age was estimated for 80 of
them. Due to the heteromyarian shell form of
the C. kusceri shell, it was not always pos-

TABLE 2. Congeria kusceri. Comparison of the estimated von Bertalanffy growth parameters for the total sample of all individuals obtained from the pit Jama u Predolcu during 2009 with respect to sex. Values are presented as means + standard deviations (minimum-maximum). L. asymptotic length; К, growth constant; to, initial condition parameter; r2, coefficient of determination; 2', growth performance index.

Shell length Age Le K to
n (mm) (years) (mm) (year) (year) r2 O'

Males 44 VE РЕГ 16.7 0.04 -3.69 0.924 1.05
(6.6-15.4) (11-53)

Females 38 12.1 + 3.4 28.4 + 12.9 18.7 0.04 -2.31 0.912 1.14
(6.5-17.0) (9-51)

Hermaphrodites 1 ¡Ae 26

Total 80 (154 3:0 27.8 +127 18.2 0.03 -3.96 0.908 1.01
(6.5-17.0) (9-53)

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Shell length (mm)

Percentage

25 30 60

Age (years)

95 à 40: 45 5 55

ЕС. 6. Сопдепа kusceri. (A): Shell length; (В): Age distribution of male (black) and female (grey) indi-viduals used in this age analysis study.

sible to prepare acetate peel replicas along
the maximum growth axis, that is, from the
umbones to the postero-ventral margin ofthe
shell valve (Fig. 2A: a, b), as used for marginal
growth increment analysis and ageing (Fig. 2A: c, d). This was particularly problematic for ten smaller individuals used for marginal growth analysis, and it was thus not possible to estimate their ages. Shell length and age structure data obtained for the C. kusceri in-

dividuals used in the age analysis component of this study are presented in Figure 6. The population growth curve data generated for C. kusceri from the length-at-age data are shown in Table 2 and illustrated in Figure 7. Analysis using ANCOVA showed that there was a statistically significant difference in the age structure of individuals with respect to sex when shell length was used as the covariate (Fi 78 = 4.07, pe 0.047).

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FIG. 7. Congeria kusceri. Von Bertalanffy growth curves for (A): The total sample; (B): Males; (C): Female individuals. Collected during 2009.

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DISCUSSION

Karatayev et al. (2006) noted that in tem-perate regions, shell growth by Dreissena polymorpha (Pallas, 1771) ceases in winter and resumes each spring after an increase in water temperature. Results of our study identify the same growth pattern for C. kusceri, despite its occupation of subterranean waters. That is, the annual pattern of growth line formation in C. kusceri coincided with an increase in water temperature, which occurs in the pit Jama u Predolcu from May to June. A water tem-perature of 13-14°C has been identified as the lower limit for both the initiation and cessation of shell growth and the reproductive maturity of C. kusceri, since the annual pattern of growth ring formation coincides with the spawning period (Morton & Puljas, 2013). It can thus be concluded that an increasing temperature is the main regulator of shell growth in C. kusceri but it is also the primary factor triggering and co-ordinating reproductive timing (Puljas, 2012). It has been further demonstrated that the annual pattern of growth expressed by C. kusceri is related to variations in alkalinity. Several studies have recorded that increases in alkalinity and a high requirement for calcium may be associated with growth in D. polymor-pha (Ramcharan et al., 1992; Vinogradov et al., 1992; Barbiero et al., 2006). Our data indicate that calcium uptake by C. kusceri coincides with a decrease in the alkalinity of the pit water. This observation, however, needs physiological elaboration as well as investigation of other factors that might be responsible for such a decrease in alkalinity.
Unlike D. polymorpha and C. kusceri, growth of Mytilopsis leucophaeata (Conrad, 1831) oscillated each year and comprised a single phase of major growth from late spring until summer, followed by a second period of minor growth in autumn and winter (Verween et al., 2010).
A statistical analysis of the expression of sexuality exhibited by 280 individuals of C. kusceri collected monthly from the pit, during 2009, suggested a slight sexual dimorphism (Puljas, 2012). According to that study, females were statistically significantly larger than males, although observed shell lengths of the former (5.3-17.0 mm) were relatively similar to those of the latter (4.0-15.4 mm). The differences between males and females in terms of age structure calculated in this study have been shown to differ with respect to shell length, the

males being somewhat smaller than females, as previously concluded by Puljas (2012). This study shows that the population of C. kusceri in the Jama u Predolcu pit is charac-terized by an impressive longevity of 53 years. The oldest individual was a male of 14.3 mm shell length, which compares well with the longevity estimate obtained by Morton et al. (1998) for an age of between 30 to 40 years for C. kusceri at ~ 17 mm shell length. Calcu-lations of growth rate obtained from this study suggested a maximum theoretical shell length (|...) of 16.7 mm for males and 18.7 mm for fe-males. Morton et al. (1998), however, identified С. kusceri individuals with shell lengths ranging from 9 to 24 mm. The longevity of this species is, therefore, greater than that identified in this study and such individuals will be much older than the 53 years assigned to the individuals reported upon herein.
Obtained estimates of the growth constant (k) for C. kusceri are relatively low for both sexes (0.04 year!) and similar to k-values obtained for other long-lived bivalves, such as the freshwater unionids Margaritifera margari-tifera Linnaeus, 1758 (К = 0.023-0.075 year-1; Hastie et al., 2000) and Megalonaias nervosa (Rafinesque, 1820) (К = 0.04-0.092 year-'; Christian et al., 2000; Haag & Rypel, 2010) and some marine bivalves such as Arctica islandica Linnaeus, 1767 (К = 0.02—0.06 уеаг-1; Kilada et al., 2007) and Glycymeris glycymeris (Linnaeus, 1758) (К = 0.11 and 0.13 year-1; Savina, 2004). Such values are characteristic of slow-growing and long-lived species (Beverton & Holt, 1959).
In accordance with the rate-of-living/free radical theory of ageing, sedentary bivalve molluscs are some of the longest living ani-mals (Abele et al., 2009; 2010; Buttemer et al., 2010). An age of ~ 200 years was recently documented for G. glycymeris by Reynolds (2011) while Wanamaker et al. (2008) has identified individuals of A. islandica that were estimated to be ~ 400 years old. Both of these latter species occur in subtidal marine habitats and are relatively large, that is, a shell length of ~ 9 cm for С. glycymeris (Reynolds, 2011) and ~ 12.5 cm for A. islandica (Morton, 2011). Although these bivalves are often referred to as “large”, they are nowhere near as large as giant clams, for example, the ‘small’ giant clam Tridacna maxima Rodding, 1798, which lives for only ~ 30 years (Romanek, 1987). It thus seems that adult size probably has little or no relationship with longevity, at least in the sea,

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and that other features of a species’ biology
can better explain the phenomenon of bivalve
extreme longevity investigated only relatively recently.
But what is the situation in freshwater bivalve
species? In comparison with other representa-tives of the Dreissenidae, C. kusceri has sig-nificantly smaller shell length values but greatly expanded longevity. In England, for example, D. polymorpha can attain a shell length of 50 mm and live for five years, although a general longevity of 3.5 years is normal (Morton, 1969). Similarly, maximum shell lengths of 22 mm (Verween et al., 2010) and 25.2 mm (Kennedy, 2011), and a longevity of between 2 to 4 years has been recorded for M. leucophaeata (Ver-ween et al., 2010), while the equivalent figures for its congeneric, M. sallei, are 29 mm and < 2 years (in Hong Kong) (Morton, 1989).
Also in Hong Kong, the freshwater unionid Sinanodonta woodiana (Lea, 1834) attains a maximum theoretical shell length of ~162 mm and has a life span of ~ 12 years (Dudgeon & Morton, 1983). This compares well with life span estimates of between 10 to 15 years for unionids in the River Thames in England (Negus, 1966). But some unionids can reach impressive longevities, such as Margaritifera margaritifera, which can reach an age of 100-200 years (Bauer, 1992; Ziuganov et al., 2000; Haag & Rypel, 2010) and Elliptio compla-nata (Lightfoot, 1786) and Lampsilis siliquoidea (Barnes, 1823) both with longevities of > 150 years (Anthony et al., 2001). Further, Helama & Valovirta (2008) considered that, in Finland, if not anthropogenically disturbed, M. mar-garitifera may reach super-centenarian ages with the oldest perhaps attaining > 200 years. In Japan, the congeneric Margaritifera laevis Haas, 1910 attains shell lengths of between 111 to 133 mm and lives for between 36 to 67 years (Awakura & Sugiwaka, 1988; Akiyama & Iwakuma, 2009).
The longevity values obtained for the ma-rine and freshwater species identified above can, in some instances, indicate an extremely slow growth rate. Among the Dreissenidae, C. kusceri is the only species that displays such an extreme longevity, presumably because of its underground habitat and adaptations that uniquely fit it and, possibly, its congeners (BilandZija et al., 2013) for such a troglodytic

life style. Furthermore, achieving a shell length of less than half that of its short-lived cousins Dreissena and Mytilopsis, С. kusceri too must have an extremely slow growth rate in com-parison to their fast ones. According to Culver (1982), nearly all cave organisms for which any data are available show either some or all of the following characteristics: delayed reproduction, low fecundity, larger eggs and increased longevity. Such features are com-monly associated with K-selection (Pianka, 1970) and, as discussed herein and by Morton & Puljas (2013), C. kusceri would seem to fit such a definition, in contrast to its opportunistic, r-selected, confamilial cousins Dreissena and Mytilopsis.
But what attributes does C. kusceri possess that allow it to live for so long? Certainly, there is а general absence of molluscivorous preda-tors in its highly subterranean environment but, perhaps, just as importantly, Morton & Puljas (2013) have demonstrated that the species exhibits a low fecundity, highly specialized larval brooding resulting in only “occasional” low-level recruitments, retrieval by resorption of unfertilized gametes, and no loss of repro-ductive abilities with age. That is, by adapting to, in evolutionary terms, over the last 22-23 million years (BilandZija et al., 2013), and opti-mizing the constraints imposed by occupation of a subterranean habitat on the individual, the species has survived by reducing the effects and consequences of physiological ageing thereby nullifying reproductive senescence (Morton & Puljas, 2013). The recent discovery of an unique ‘flock’ of subterranean species of Congeria (BilandZija et al., 2013), of which C. kusceri is but one, has thrown new light on how colonization and continued and successful oc-cupation of such a freshwater habitat has been achieved, adding further complexity to an ongo-ing story of amazing vicariant evolution.

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